Minimizing inter-genotypic competition effects to predict genetic values and selection in forestry genetic tests

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ABSTRACT: The effect of competition is an important source of variation in breeding experiments. This study aimed to compare the selection of plants of open-pollinated families of *Eucalyptus* with and without the use of competition covariables. Genetic values were determined for each family and tree and for the traits height, diameter at breast height and timber volume in a randomized block design, resulting in the variance components, genetic parameters, selection gains, effective size and selection coincidence, with and without the use of covariables. Intergenotypic competition is an important factor of environmental variation. The use of competition covariables generally reduces the estimates of variance components and influences genetic gains in the studied traits. Intergenotypic competition biases the selection of open-pollinated eucalypt progenies, and can result in an erroneous choice of superior genotypes; the inclusion of covariables in the model reduces this influence.

Keywords: *Eucalyptus* spp., covariable analysis, selection gains

Introduction

The possibility of predicting gains is considered one of the greatest contributions of quantitative genetics to breeding (Falconer and Mackay, 1996). When different selection criteria are considered, the prediction of gains for each criterion is important as an orientation for breeders on how to use the available plant material to obtain maximum gains for the traits of interest (Paula et al., 2002). However, these gains assessed by the most recognized methodologies are not consistent with the real biological event in the trials for selection, since most commercial eucalyptus stands are monoclonal plantations where the competition capacity of plants is identical, unlike in the experimental tests where there is intergenotypic competition due to the proximity of experimental plots with different genotypes. Therefore, the conditions of selection of genotypes differ from those of commercial stands, which may affect the success of selection.

The success of a breeding program of perennial species depends on the knowledge of the final product of interest and methods of selection and breeding, and particularly on an efficient use of the techniques of quantitative genetics (Resende, 2002). Since competition is an important source of experimental variation it should be included in the experimental statistical models to estimate the genetic value of treatments, free of this effect.

It is possible to discriminate the effects of competition in testing of forestry breeding, but genetic-statistical models that fit the data of the response variables are required, minimizing the bias caused by the unequal development of the neighborhood (Leonardecz Neto et al., 2003). Thereby, the statistical analysis should reflect the biological event accordingly, which is not perfectly described by the usual analysis. In the models used for data analysis of genetic testing to select superior genotypes, it is not common to include the effects of competition, since no routine tests and/or applications were developed for this purpose. Therefore, routines must be tested to minimize or even eliminate the effect of intergenotypic competition in forestry genetic trials (Scarpinati et al., 2009).

As the competition effect represents an essential source of variation, this study aimed to compare the selection of trees from open-pollinated *Eucalyptus* families with and without the use of covariables of competition.

Materials and Methods

The trials of progenies were installed in Guatapará, state of São Paulo, Brazil (21°29' S, 47°58' W). Experiment 1 (EXP1) was initiated in 1996 and experiment 2 (EXP2) in 1999. The growth in height (H) and circumference at breast height (CBH) of seven-year-old trees were evaluated. Based on the measurement of CBH the diameter at breast height (DBH) was determined and, the timber volume with bark (VOL) for each diameter class was calculated with the shape factor:

$$VOL = \left(\frac{(DBH)^2 * \pi * H}{4}\right)F$$

where: VOL= timber volume with bark (m^3); DBH= diameter at breast height (m); H= height (m); F= shape factor of diameter class adopted by the company.

The experimental design was a randomized complete block with six replications in both experiments. EXP1 consisted of four controls (clones of *Eucalyptus grandis x Eucalyptus urophylla*) and 49 treatments (open-pollinated families of *Eucalyptus grandis*) and EXP2 comprised 44 treatments (open-pollinated families of *Eucalyptus grandis* × *Eucalyptus urophylla*). The plots were arranged linearly, containing 10 plants each all being considered, totaling 3180 plants in EXP1 and 2640 in EXP2, spaced 3.0 × 2.5 m, forming a progeny test plantation of 2.385 ha in EXP1 and of 1.98 ha in EXP2. Plots were so arranged that, neighbors of each plot belong to the adjacent plots, which consist of 10 plants each and are located in the same block. The upper and downer neighbor of the object tree does also belong to the same plot, exception made for the first and last plot plants, since these plants are part of the former or later block (Figure 1).

The progenies were evaluated based on data from surviving plants of the experiments. The performance, breeding value of each family and plant for the studied traits (timber volume in m^3 - VOL, trunk height, in m - H and diameter at breast height, in cm - DBH) were determined by the linear mixed model by the REML procedure - REML for DBH and H in both experiments, and for VOL in EXP1. For VOL in EXP2 the procedure MIVQUE0 was used, since by REML there was no convergence to estimate the maximum likelihood. Therefore, it was not possible to estimate the breeding values of individual plants. Subsequently, two covariables of competition were added to these models, as described below:

Competition index of Hegyi (Hegyi, 1974):

This index is the weighted distance aggregate of the rays of competition by the forestry trait of the trees considered competitors in relation to the target tree.

$$CI_i = \sum_{j=1}^{n} (D_j / D_i) / Dist_{ij}$$

where: CI_i = competition index of tree *i;* D_j/D_i = value of the forestry trait of competitor j expressed in relation to the forestry trait of the target tree i; $Dist_{ij}$ = distance between the competitor j and the target tree i; n = number of competing trees. In this equation the eight nearest neighbor trees (competing) were taken into consideration.

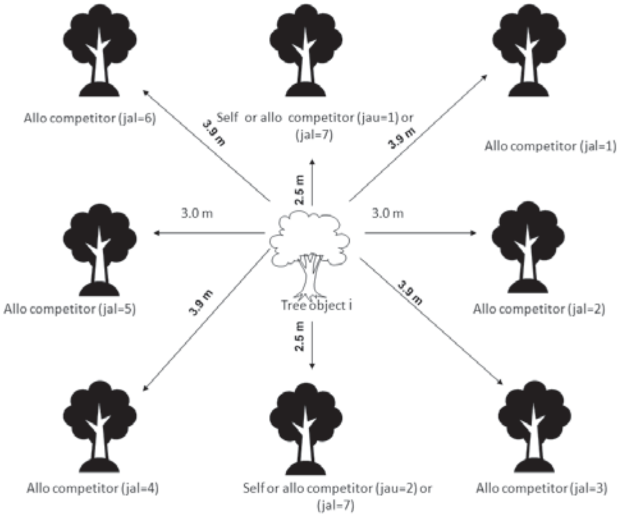

Figure 1 – Arrangement of the trees competing for the calculation of covariates.

Mean of self-competition (MSC):

Arithmetic mean of the forestry trait of the self-competing trees (according to the Figure 1), given by:

$$MSC = \sum_{j=1}^{n} j_{au} / n$$

where: j_{au} = value of the forestry trait of the self-competitive tree, n = number of self-competitive trees.

The BLUP procedure adjusts the data to the observable environmental effects, such as block, and simultaneously predicts the genetic value. In the case of this study, BLUP predicted the genetic values of the families adjusted for blocks, CI and MSC as well as the genetic values of individual plants adjusted for blocks and families (Resende, 2002). Thus, the genotypic values of individual plants are adjusted for blocks and take the merits of the family into account.

The families were assessed for each trait and their classification was compared, with and without the use of covariables of competition, to infer how competition affects the classification of families, and the influence on the different traits. A selection intensity of 4 % per trial was determined for each trait, with selection based on breeding values of trees with or without the inclusion of the covariables of competition. The performance of trees in each situation and the influence of competition on each studied trait were compared. The selection was made with the intention of cloning superior trees and takes them to a clone test.

The statistical analyses were run on SAS (1999) by the procedure Proc Mixed and the methods REML and MIVQUE0, with and without the use of covariables. The covariance analysis by the linear mixed model was adjusted simultaneously with the prediction, so only the inclusion of the covariables in the routine analysis was required.

Traits were evaluated for genetic parameters and their components of variance and descriptive statistics for the progenies are not considering the controls in the model (overall mean (OM), heritability among (h_f^2) and within (h_{wf}^2) the families and total heritability (h_t^2); mean of the selected population (MSP), selection differential (SD = MSP - OM), selection gain (SG = SD * h_t^2 and as a percentage of the overall mean (SG%=((SD* h_t^2)/OM)*100), genotypic variance among ($\hat{\sigma}_{gf}^2$) and within ($\hat{\sigma}_{gwf}^2$ the families, experimental error among ($\hat{\sigma}_e^2$) and within ($\hat{\sigma}_{ew}^2$) the plots and effective population size of the improved population (N_e) and selection coincidence (Coinc), with and without the use of covariables. The error and coefficient of variation within plots of EXP1 were estimated with data of the controls (clones) generating a pure error, without the presence of genotypic variance. In EXP2 the genotypic variation within families was estimated by calculating the percentage of each component in relation to the total variance of EXP1. This percentage was used to calculate the error within plots in EXP2. Genotypic variance within families was estimated by subtracting the other components of variance ($\hat{\sigma}_e^2$, $\hat{\sigma}_{gf}^2$ and $\hat{\sigma}_{ew}^2$) from the total variance observed in EXP2. The within-plot error in EXP2 has therefore the same magnitude as the total variance in EXP1.

The effective population size was estimated based on the inbreeding level, in which

$$F_t = \left(\frac{1}{2N_e}\right) + \left(1 - \frac{1}{2N_e}\right)F_{t-1}$$

for generation t. Whereas $F_{t-1} = 0$ then $F_t = 1/(2N_e)$, therefore $N_e = 1/(2F)$, according to Falconer and Mackay (1996). Based on this principle, Morais et al. (1997) derived the following expressions used in this study:

$$F_{FMI_{IZ}} = \frac{1}{2\sum Ns}\left[(1 + F_a) + (n_{iz} - 1)r\right]$$

$$F^*_{FMI_Z} = \frac{\sum_z^1 F_{FMI_Z}}{p^*_Z}$$

$$N_e = \frac{1}{2F^*_{FMI_Z}}$$

where: $F_{FMI_{IZ}}$ = Inbreeding coefficient estimated for family *i*, for trait z, in the selection using genotypic values estimated by the linear mixed model by the methods REML and MIVIQUE0; *Ns* = Number of selected plants in the experiment; F_a = Inbreeding coefficient of selected plants; n_{iz} = Number of plants selected for trait z, in family *i,* in the selection using genotypic values estimated by linear mixed model by REML and MIVIQUE0; *r* = Coefficient of genotypic intraclass correlation; $F^*_{FMI_Z}$ = estimated mean inbreeding coefficient for trait z, in the selection using genotypic values estimated by the linear mixed model by REML and MIVIQUE0; p^*_Z = number of selected families for trait z, in the selection based on genotypic values estimated by the linear mixed model by REML and MIVIQUE0, and N_e = Effective population size.

For the application of the above equations, it was assumed that: (i) the inbreeding coefficient of selected plants (F_a) is zero, since it is an F_1 population, and to determine the real value of this variable it would be necessary to know the genealogy of the progenies; and (ii) the coefficient of genotypic intraclass correlation (*r*) for half-sib families is 0.25.

The selection coincidence is the percentage of the total number of selected trees of the coincident plants in both conditions for each trait. To obtain estimates of variance components and heritability the families were assumed to be half-sibs.

Results and Discussion

The studied covariables proved consistent since the coefficient of linear regression was uniform for all traits. The Competition Index of Hegyi (CI) had a negative regression coefficient, i.e., the taller the neighbor trees, the shorter the target plant. The mean for self-competition also had a negative coefficient, but lower than CI. No interaction with families was observed for the two covariables, demonstrating that a single slope of the straight line was enough to correct or analyze the covariables. However, CI can only be used after removal of the tree data growth much lower (outliers) than the average of the experiment, and perhaps individuals with high probability of death, but after removing the values for these trees this covariate did not show significantly more interaction with the treatments.

In a similar way, the covariables interfered by the analysis, reduced the value of the variance components of almost all traits except in EXP1 (where the genetic variability within families increased for tree height), and in EXP2 (for DBH for both genotypic variances and for H for the error among plots). In general, heritability increased, except in EXP2 for the trait VOL which presented a small reduction, showing that the covariables interfered by the results of the analysis improved the environmental control at a higher proportion than the reduction of genetic variability (Table 1).

The intergenotypic competition interferes with genetic experiments in both the magnitude of the difference between the genotypes as well as the environmental error. Therefore, genotypes considered superior in the usual analysis, disregarding the competition effect, may no longer be superior after the inclusion of competition covariables, if they are highly competitive and had benefitted from the low productivity of their neighbors. Other authors observed the same effect of intergenotypic competition. Leonardecz Neto et al. (2003) in experiments with forest tree species also observed a reduction of genetic variability and experimental error after the application of competition covariables in the statistical model. In experiments with designs that favor intergenotypic competition, the genetic variability and experimental error tend to be greater (Scarpinati et al., 2009). The higher degree of blocks x treatments interaction was therefore attributed to competition, since in a given block the genotype under study may have been allocated next to uncompetitive plants and in another block next to very competitive plants. This may also be the case within plots, since in this test of open-pollinated families, neighboring plants are "genetically different".

A comparison of the selection gain with and without the use of covariables of competition showed that in most cases gains were lower after applying the covariables, indicating a reduced difference among the genotypes (Table 1). This reduction in gains was expected and desired, since it is known that selected genotypes do not have the same productivity mean yield when transferred to commercial stands. The results including competition covariables in the selection are therefore possibly closer to the reality of commercial production. The drop of the selection differential was more significant than the reduction of genetic gain, mainly because in most cases heritability increased.

Competition is an important factor to challenge more competitive plants. When families with a low level of competition are exposed to a mean competition level in relation to the experiment, many of the trees selected before may not keep on being afterwards, giving an opportunity to some other family plants.

The ranking and the means of the best 20 tree families of the two experiments (Table 2) show that the best families are the same with minor shifts in the 20 superior progenies, ranging from one family, for VOL in EXP1 and DBH in EXP2,

Table 1 – Variance components and related parameters, with and without the use of covariables of competition, for the traits height (m), diameter at breast height (DBH, cm) and timber volume (m^3), in two experiments of open-pollinated eucalyptus progenies.

Variance components and Genetic parameters	TRAITS					
EXP1	HEIGHT		DBH		VOLUME	
Use of cov.	without	with	without	with	without	with
$\hat{\sigma}^2_{gf}$	4.20	2.10	4.58	1.64	0.0038	0.0020
$\hat{\sigma}^2_{gwf}$	4.76	6.19	9.01	4.36	0.0043	0.0028
$\hat{\sigma}^2_{e}$	3.10	0.98	0.69	0.44	0.0012	0.0008
$\hat{\sigma}^2_{ew}$	11.54	3.23	8.24	3.08	0.0084	0.0047
$\hat{h}_f^2$	22.28	33.33	33.89	31.75	28.36	26.66
$\hat{h}_{wf}^2$	24.55	59.53	50.21	55.33	30.69	33.99
$\hat{h}_t^2$	37.97	66.34	60.34	63.01	45.76	46.60
OM	20.10	20.10	14.38	14.38	0.181	0.181
MSP	24.16	23.43	20.53	17.92	0.354	0.328
SD	4.06	3.33	6.15	3.54	0.17	0.15
SG (SG in %)	1.54 (7.66)	2.21 (12.5)	3.71 (25.8)	2.23 (15.5)	0.08 (43.7)	0.07 (37.7)
CV%	23.62	12.49	19.96	12.19	36.36	27.20
EXP2						
$\hat{\sigma}^2_{gf}$	1.30	0.69	0.51	0.77	0.00084	0.00031
$\hat{\sigma}^2_{gwf}$	9.07	5.37	8.98	9.38	0.0081	0.0041
$\hat{\sigma}^2_{e}$	0	0.666	1.180	0.532	0	0.00033
$\hat{\sigma}^2_{ew}$	9.93	2.34	6.16	5.10	0.0081	0.0040
$\hat{h}_f^2$	11.49	18.59	6.47	12.01	9.44	6.83
$\hat{h}_{wf}^2$	47.77	64.10	55.04	62.49	50.07	48.75
$\hat{h}_t^2$	51.09	66.82	56.39	64.31	52.54	50.61
OM	23.19	23.19	15.44	15.44	0.230	0.230
MSP	28.79	26.85	22.5	22.31	0.529	0.450
SD	5.600	3.660	7.060	6.870	0.299	0.220
SG (SG in %)	2.86 (12.3)	2.45 (10.6)	3.98 (25.8)	4.42 (28.6)	0.16 (69.6)	0.11 (47.8)
CV%	13.59	6.60	16.07	14.62	39.09	27.34

$\hat{\sigma}^2_{gf}$ - genotypic variance among families; $\hat{\sigma}^2_{gwf}$ - genotypic variance within families; $\hat{\sigma}^2_{e}$ - experimental error among plots; $\hat{\sigma}^2_{ew}$ - experimental error within plots; $\hat{h}_f^2$ - heritability among families; $\hat{h}_{wf}^2$ - heritability within families; $\hat{h}_t^2$ - total heritability; OM - overall mean; MSP - mean of selected population; SD - selection differential; SG - selection gain; CV% - coefficient of experimental variation .

to three families for the remaining traits in both experiments. Most changes occurred at the bottom of the table, i.e., the selected families remained the same. However, there was an intense rearrangement of positions among the 20 best families. In EXP1, the ranking of family 30 improved in all traits and the ranking for, H, DBH and VOL of family 12 rose four, six and two positions, respectively. An example of a stable family is 46, also in EXP1, which maintained its ranking almost unchanged, showing that the performance of this family was not affected by competition. The change in the top positions was always caused by a proportionally smaller production loss; all superior families were less productive after the inclusion of competition covariables than the other families, suggesting that the families whose productivity was little reduced after covariable analysis was closer to the competition mean of the experiment in the different plots, gaining positions in the rankings.

In EXP2 the shifts in ranking were less intense; some families maintained the same position or changes, if any, were not more than one or two positions in most cases. These results show that the level of competition in EXP2 was in general similar. The change caused in the classification of families in the two experiments by the use of covariables of competition was different among traits, indicating that competition affects them differently. The height was most affected by competition, with more changes in families than of DBH and VOL. However, this intense change in positions may be due to small differences between genotypes for height, so any small change in growth is more likely to change the ranking.

The averages of all traits, except for DBH in EXP2, were reduced by the inclusion of competition covariables. These decreases were most significant for DBH and VOL in EXP1 and VOL in EXP2, so that the most productive families were

Table 2 – Ranking of the 20 best open-pollinated eucalyptus families, their genotypic values (in brackets) and standard error (SE) in two experiments for the traits height (m), diameter at breast height (DBH, cm) and timber volume (m^3), with and without inclusion of covariables of competition.

Trait	Height		DBH		Vol	
Use of the covariable	without	with	without	with	without	with
	------------- m-------------		------------- cm -------------		------------- m^3 -------------	
Classification			EXP1 Families (Means)			
1	29 (24.56)	29 (23.14)	29 (19.09)	30 (16.99)	29 (0.319)	30 (0.277)
2	03 (23.99)	02 (22.87)	03 (18.74)	29 (16.94)	03 (0.310)	29 (0.276)
3	02 (23.88)	03 (22.68)	30 (18.43)	03 (16.46)	30 (0.305)	03 (0.270)
4	04 (23.39)	30 (22.56)	04 (18.40)	04 (16.44)	04 (0.303)	04 (0.267)
5	06 (23.25)	46 (22.42)	46 (17.82)	46 (16.44)	46 (0.281)	46 (0.255)
6	46 (23.22)	06 (22.39)	02 (17.52)	05 (16.31)	02 (0.267)	31 (0.246)
7	30 (23.18)	05 (22.28)	05 (17.50)	06 (16.12)	05 (0.264)	05 (0.239)
8	05 (23.07)	04 (22.07)	06 (17.35)	02 (16.03)	06 (0.262)	02 (0.233)
9	09 (22.32)	31 (21.81)	31 (16.71)	31 (15.97)	31 (0.259)	06 (0.231)
10	31 (22.23)	09 (21.72)	01 (16.22)	32 (15.35)	08 (0.232)	07 (0.223)
11	01 (21.97)	32 (21.52)	09 (15.98)	09 (15.25)	01 (0.229)	08 (0.222)
12	32 (21.83)	12 (20.97)	08 (15.94)	12 (15.19)	07 (0.225)	32 (0.216)
13	48 (21.74)	01 (20.71)	32 (15.67)	08 (15.15)	09 (0225)	09 (0.207)
14	47 (21.48)	08 (20.52)	47 (15.47)	34 (15.01)	32 (0220)	12 (0.202)
15	07 (21.21)	48 (20.49)	36 (15.46)	36 (14.74)	47 (0.212)	01 (0.195)
16	12 (20.85)	07 (20.39)	07 (15.40)	19 (14.74)	12 (0.200)	47 (0.186)
17	08 (20.72)	11 (20.25)	48 (15.07)	07 (14.67)	36 (0.195)	48 (0.186)
18	11 (20.19)	40 (20.11)	12 (14.93)	35 (14.61)	19 (0.190)	33 (0.184)
19	36 (20.10)	19 (20.06)	19 (14.58)	48 (14.55)	48 (0.184)	34 (0.184)
20	41 (19.78)	28 (20.01)	33 (13.98)	11 (14.43)	33 (0.163)	19 (0.179)
SE	0.5613	0.3708	0.6069	0.3507	0.0175	0.0133
Classification			EXP2 Families (Means)			
1	36 (25.53)	36 (24.82)	37 (16.59)	37 (17.09)	37 (0.287)	37 (0.263)
2	42 (25.03)	09 (24.50)	42 (16.43)	42 (16.95)	36 (0.280)	36 (0.259)
3	37 (24.64)	37 (24.18)	36 (16.32)	36 (16.73)	42 (0.278)	09 (0.256)
4	41 (24.52)	42 (24.17)	08 (16.19)	08 (16.62)	09 (0.266)	42 (0.254)
5	35 (24.50)	34 (24.11)	09 (16.15)	09 (16.54)	08 (0.263)	34 (0.253)
6	08 (24.45)	41 (24.10)	43 (16.06)	43 (16.37)	43 (0.259)	8 (0.247)
7	34 (24.44)	35 (24.07)	35 (16.00)	34 (16.23)	35 (0.258)	11 (0.246)
8	43 (24.37)	39 (24.07)	19 (15.97)	19 (16.21)	32 (0.256)	43 (0.242)
9	09 (24.32)	08 (24.07)	34 (15.92)	35 (16.17)	34 (0.254)	32 (0.240)
10	32 (24.17)	40 (23.98)	41 (15.86)	41 (16.08)	19 (0.252)	35 (0.240)
11	19 (23.83)	38 (23.94)	14 (15.85)	39 (15.95)	14 (0.249)	14 (0.239)
12	14 (23.80)	32 (23.93)	44 (15.77)	14 (15.89)	41 (0.248)	04 (0.238)
13	38 (23.68)	43 (23.85)	27 (15.75)	44 (15.81)	20 (0.240)	20 (0.238)
14	15 (23.65)	33 (23.64)	39 (15.72)	27 (15.74)	44 (0.239)	21 (0.238)
15	39 (23.62)	14 (23.61)	04 (15.60)	20 (15.65)	15 (0.238)	27 (0.236)
16	33 (23.57)	11 (23.49)	28 (15.58)	15 (15.65)	27 (0.237)	19 (0.236)
17	20 (23.52)	28 (23.39)	20 (15.57)	28 (15.63)	39 (0.235)	44 (0.235)
18	40 (23.38)	04 (23.33)	15 (15.56)	40 (15.63)	04 (0.234)	23 (0.232)
19	28 (23.28)	18 (23.30)	12 (15.48)	12 (15.62)	28 (0.233)	41 (0.232)
20	04 (23.14)	05 (23.25)	30 (15.42)	04 (15.53)	21 (0.229)	40 (0.231)
SE	0.5649	0.4521	0.5089	0.5174	0.0131	0.0092

favored by a lower level or even the absence of competition, when there were failures in adjacent plots. The effective size (N_e) of the selected population increased significantly for the three traits in EXP1 and for H in EXP2; for DBH in EXP2 there was a slight drop and VOL remained unchanged. This fact is of utmost importance for breeding, because the effective size of the base population is the limiting factor in advanced generations. In EXP2, since the genetic variability within families was much higher than variability among families, the selection of trees of different progenies was favored resulting in a high N_e, even without the use of competition covariables, hampering a significant increase in N_e by the inclusion of the covariables (Tables 3 and 4).

In EXP1 (Table 3), regardless of the trait, the families with most selected plants in the selection without covariables of competition were all less represented after the inclusion of competitive covariables in the analysis. This effect was most significant for H, since trees of only five families had been selected, so that selection, without the use of competition covariables, favored the selection of the tallest families. When comparing the numbers of trees selected per family with selection coincidence (Table 3), the latter was high, indicating that the selected trees of a family were practically the same by both methods. The trees selected after the inclusion of competition covariables in the analysis and that had not been selected before were mainly from families not represented in the previous selection. For DBH this exchange was more intense, reducing the value of coincidence.

In EXP2 (Table 4), both the number of selected families as the representativeness of each of these were little changed, with most significant changes for H. The changes in selected populations, as well as positions in ranking of trees and families show that intergenotypic competition is an important factor of variation, which may favor or not a genotype or family. When covariables are applied in the mathematical model to correct this bias the distortion seems to be reduced.

Several authors have described the interference of the intergenotypic competition on the estimates of variance components, and indicate that when correction covariables of this effect are applied this influence can be reduced to a greater or lesser degree, depending on the crop and methodology. Cargnelutti Filho et al. (2003) reported reduced environmental variation and an improvement in the discrimination of cultivars in maize trials. Duarte and Vencovsky (2005), however, mentioned that spatial analysis resulted in a different ranking of the lines compared to non-spatial analysis, and finally in a reduced influence of effects of local variation on selection. Costa et al. (2005) reported that the inclusion of covariables, mobile averages and papadakis, generally improved the original model chosen for common bean cultivar selection.

In perennial plants the same effects were detected by some authors. Leonardecz Neto et al. (2003) reported the same effect at varying degrees in native and exotic forests for tests of progenies and origins. Scarpinati et al. (2009) reported increased competition and minor shifts in the ranking of eucalyptus clones when using designs that favor competition.

In general, intergenotypic competition is an important source of variation in progeny tests of *Eucalyptus*, so that not taking it into consideration may result in an erroneous selection and identification of superior trees. The competition effect was pronounced in the three traits and the inclusion of covariables of competition altered both the ranking of trees and families as well as the estimates of genetic parameters and

Table 3 – Number of selected plants per open-pollinated *Eucalyptus* family in EXP1, Effective size (N_e) and Coincidence (Coinc.) of selected trees, with and without using competition covariables, for the traits height, diameter at breast height (DBH) and timber volume.

Trait	Height		DBH		Volume	
Family	Use of the covariable		Use of the covariable		Use of the covariable	
	without	with	without	with	without	with
1	-	-	2	-	1	1
2	25	15	2	4	2	2
3	32	9	16	9	19	16
4	7	4	15	7	19	11
5	-	7	6	8	5	6
6	-	5	6	7	5	5
7	-	-	5	3	5	5
8	-	1	4	4	3	4
9	-	4	1	1	1	1
11	-	1	-	-	-	-
12	-	1	3	4	2	3
18	-	-	-	1	-	-
19	-	-	1	3	-	1
23	-	-	-	2	-	2
24	-	-	-	1	-	-
27	-	1	-	-	-	-
28	-	-	-	1	-	-
29	52	17	18	13	23	18
30	2	21	17	14	19	17
31	-	8	5	11	4	7
32	-	6	-	5	-	1
33	-	-	-	1	-	2
34	-	1	-	1	-	1
35	-	-	-	1	-	-
38	-	1	-	1	-	-
39	-	-	1	1	-	1
40	-	-	-	2	-	-
41	-	-	1	2	-	2
45	-	-	-	2	-	-
46	-	12	13	6	10	10
47	-	-	1	-	-	1
48	-	4	1	3	-	1
N_e	17.74	49.40	51.25	63.09	41.30	58.05
Coinc.	35.6		65.3		83.9	

Table 4 – Number of selected plants per open-pollinated eucalyptus family in EXP2, effective size (N_e) and Coincidence (Coinc.) of selected trees, with and without using competition covariables, for the traits height, diameter at breast height (DBH) and timber volume.

Trait	Height		DBH		Volume	
Family	Use of the covariable		Use of the covariable		Use of the covariable	
	without	with	without	with	without	with
	------- m -------		------- cm -------		------ m^3 ------	
1	3	1	2	1	1	2
2	6	6	4	4	4	3
3	2	2	3	3	2	3
4	3	2	4	5	6	6
5	2	2	4	4	4	4
6	5	3	3	4	2	2
7	2	3	1	1	-	-
8	-	-	2	2	2	2
9	1	1	2	2	2	2
10	-	1	2	2	1	1
11	5	6	3	3	3	4
12	2	4	1	4	1	2
13	2	1	1	-	-	-
14	-	-	1	1	-	-
15	1	1	5	3	5	4
16	2	1	1	1	1	2
17	7	4	3	3	3	3
18	6	2	2	2	2	1
19	-	3	3	2	3	2
20	3	2	6	6	5	6
21	4	4	3	2	4	5
22	9	5	4	3	4	1
23	8	6	3	3	5	3
24	3	3	1	-	-	-
25	-	2	1	2	1	1
26	1	-	1	1	1	1
27	1	3	3	3	2	2
28	3	4	3	3	3	3
29	-	4	1	1	1	1
30	6	5	4	4	5	4
31	8	5	5	6	5	5
32	-	-	2	3	1	1
33	-	1	-	-	-	-
34	-	-	1	1	2	1
35	-	2	2	2	3	3
36	1	1	3	4	4	5
37	-	1	2	2	2	2
38	4	3	4	4	4	5
39	1	1	1	-	1	2
40	3	4	2	2	1	1
41	-	-	-	-	1	1
42	-	-	3	2	3	4
43	-	4	1	1	2	2
44	2	3	3	4	4	4
N_e	64.90	72.29	76.76	74.15	74.15	74.15
Coinc.	54.91		86.79		89.62	

selection gains. Intergenotypic competition therefore affects the results of the selection of progeny tests of open-pollinated eucalyptus. The competition benefits mainly average trees of good families. This effect was well-demonstrated in the selection for H in which trees of few families were selected, and by the use of competition covariables more families were represented in the selection. The most promising result of the inclusion of competition covariables is directly linked to this fact, which is an increase in effective population size, since selection based on few families restricts the genetic basis and can be a complicating factor for the future of a breeding program.

By taking the competition covariables into account, the estimates of genetic gains decreased, mainly by reducing the extent of the difference between the genotypes. This suggests that the most competitive genotypes, which are also the most productive, take advantage of the low competitiveness of their neighbors. By including the competition effect in the analysis, the yield of these genotypes was reduced and that of genotypes with less competitive power, increased. This is an important finding, since the commercial plantations are now based on monoclonal stands or from the same family, where all individuals have the same or similar competition and consequently, genotypes that had been selected as highly competitive may not necessarily be highly productive.

The objective of the correction of the competition, by means of covariables, is not to select low productive and competitive genotypes. The main function of this analysis is to establish equal competition among genotypes, to at least minimize the possible beneficial effect on some genotypes which then stand out in the test because the competition level was very low. This fact is particularly important in progeny trials where the goal is to evaluate trees, which are not repeated elsewhere in the test with a different genetic constitution, and also because the neighbors are different and have a differentiated competition capacity from the other experimental situations.

Conclusions

Intergenotypic competition is an important factor of environmental variation, interfering with the selection results. The inclusion of competition covariables reduces estimates of variance components and influences the genetic gains. Intergenotypic competition biases selection of open-pollinated *Eucalyptus* progenies and can mislead the choice of superior genotypes; the inclusion of covariables in the analysis models reduces this influence.

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